The University of Chicago
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THE NERVUS TERMINALIS IN URODELE AMPHIBI

A DISSERTATION

SUBMITTED TO THE FACULTY
OF THE

OGDEN GRADUATE SCHOOL OF SCIENCE

IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF ANATOMY

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THE NERVUS TERMINALIS IN URODELE AMPHIBIA

PAUL S. McKIBBEN

From the Anatomical Laboratory of the University of Chicago

FORTY-SIX FIGURES

There has been described recently in several groups of fishes and in anuran amphibia a bundle of unmedullated nerve fibers associated with the olfactory nerve and connected with the forebrain. This bundle of unmedullated fibers has been named the nervus terminalis by Locy ('05a).

Although early figured in Galeus canis by Fritsch ('78), the n. terminalis was first accurately described by Pinkus ('94) for Protopterus. It was seen in Amia by Allis ('97) and described in twenty-seven species of selachians by Locy ('05a). In embryos of Ceratodus, Sewertzoff ('02) has described the nerve and Bing and Burckhardt ('04, '05) have recorded its presence in the adult of the same form. Brookover ('08, '10) has confirmed and supplemented the findings of Allis in Amia and has noted the presence of the nerve and associated ganglion cells in Lepidosteus. Sheldon and Brookover ('09) have reported the presence of the n. terminalis in the carp and Herrick ('09) in the frog.

A comparison of the findings in the forms above mentioned reveals the general similarity of the nerve in all cases. Differences in course and connections, however, are clearly apparent, most of which may be explained by a consideration of the form relations of the structures with which the n. terminalis is associated (see Johnston '11). Quite distinctly separate from the olfactory bulb and tract in dipnoans and selachians, the n. terminalis seems, in the ganoids, teleosts and amphibia, to be more closely associated with and in fact surrounded by olfactory fibers and comes to lie imbedded in the substance of the forebrain

for a part of its course. Its peripheral distribution, as far as our knowledge extends, is in the nasal capsule. The presence of a 'ganglion' in the course of the nerve seems quite characteristic but has not been noted in all the cases mentioned above. Its ending in the brain, where such has been described, almost always seems to be in the preoptic nucleus or in the region of the precommissural body, related to the lamina terminalis.

In Amia, Brookover ('10) describes, in addition to the connection of the n. terminalis with the forebrain, fibers 'which seem to belong to the nerve' running caudad to the region of the optic chiasma where they do not enter the brain itself but connect with the 'post-optic sympathetic system.' He shows for Amia that the ganglion cells of the n. terminalis arise together with the primary olfactory neurones from the olfactory ectodermal placode. In the carp, Brookover reports the presence of cells along the olfactory nerve which appear to form the ganglion of the n. terminalis. Sheldon ('09) describes in this form the central course of the nerve to the point where it decussates in the rostral part of the lamina terminalis. In the frog, both larval and adult, C. Judson Herrick ('09) traces the nerve from its ventro-median position in the olfactory nerve, through the glomerular zone of the olfactory bulb and ventro-median part of the hemisphere, to the region of the anterior commissure. Here there is evidence that some of its fibers end about cells of the precommissural body. Others decussate in the anterior commissure but can not be followed beyond this point. Snessareff ('10) has noted the presence of the nerve in Rana esculenta.

In connection with a discussion of the olfactory tracts of the brains of certain reptiles, C. L. Herrick ('93) mentions that in the brain of Necturus "there are a few scattered fibers on the very ventral surface which run directly caudad to beyond the chiasm—probably to the mammillary region." He states that these fibers have not elsewhere been encountered. Kingsbury ('95) notes in Necturus that "upon the ventral surface of the cerebrum several small fascicles of amyelinic fibers go caudad from the olfactory lobes to the region immediately cephalad of the mesencephalic groove (mammillary region?) where they turn

mesad and disappear." This was considered by Kingsbury to be a 'diencephalic olfactory tract' which decussated partially in the anterior commissure. The 'olfactory tract' thus described by these two authors, and well figured by Kingsbury, is undoubtedly what is considered to be the n. terminalis in this study. Bochenek ('99), in his work on the olfactory tracts of Salamandra maculosa, describes the 'tractus olfacto-commissuralis' running through the lamina terminalis to end near the preoptic recess and the 'tractus olfacto-diencephalicus' as ending in the same region. It seems probable from a study of the n. terminalis in Amblystoma tigrinum and Diemyctylus torosus, forms quite similar to Salamandra, that Bochenek was dealing here with two slips of the n. terminalis.

The specimens of Necturus maculatus used in this study were adults obtained from Alex Nielsen, Venice, Ohio. On account of the liability to injury, it was found best to apply the fixing agents before the complete removal of the brain from the skull. This was accomplished successfully, after cutting away all skin and muscle from the head, by opening the brain case both above and below before the immersion of the preparation in the fixing fluid. It was found possible in this way to preserve the form relations of the various parts more nearly as they are in the fresh condition and at the same time to insure good fixation. In some cases the fixing solutions were injected through the heart previous to the treatment as outlined above.

For the demonstration of the bundles of the n. terminalis in Necturus, staining with iron haematoxylin or Mallory's connective tissue stain was found useful after fixation in formaline-Zenker (ordinary Zenker's fluid in which the acetic acid is replaced by formaldehyde). Vom Rath's stain also gave good pictures of the nerve bundles and at the same time produced little distortion of the form relations. This method was used as follows:

Vom Rath's fluid..............3 days

sat. aq. picric acid	200 cc.
platinic chloride 10%	10 cc.
osmic acid 2%	25 cc.
glacial acetic acid	2 cc.

Wash in several changes of methyl alcohol............30 minutes
Pyrogallic acid 0.5%............2 days
Alcohol, oil of cedarwood, paraffine. Leave in alcohol several days and keep preparations in the dark during the entire procedure

The ordinary Weigert method for medullated fibers was found to show also the unmedullated bundles of the n. terminalis, easily distinguished by reason of their course and compact form.

Finer analysis of the distribution and mode of ending of the n. terminalis was accomplished by use of the Golgi silver impregnation method. Various modifications were employed but the one found most successful in this study is as follows:

Formaldehyde 10%..........24 hours
Osmium-bichromate.........3 to 6 days
osmic acid 1%..2 parts
potassium bichromate 2.5%................................8 parts
Silver nitrate 1%............3 days
Alcohol, oil of cedarwood, paraffine

Brains prepared by the Golgi method were sectioned in ribbons sixty micra thick and those prepared by other methods ten to fifteen micra thick. Sections of the brains of adult and larval Amblystoma and of the other forms described in this study were prepared by the same methods used for adult Necturus.

The author wishes to acknowledge his indebtedness to Dr. G. E. Coghill for the specimens of Diemyctylus torosus used in this study, to Dr. A. H. Wright for help in the identification of specimens, to Dr. Charles Brookover and Professor R. R. Bensley for many valuable suggestions and to Professor C. Judson Herrick, under whose direction the work has been done, for his constant encouragement and helpful counsel.

NECTURUS MACULATUS

In the brain of Necturus the n. terminalis has been recognized as a compact fascicle of fibers about 2 mm. distal to the telencephalon, embedded in the ventro-medial part of the olfactory nerve. In passing toward the brain the n. terminalis swings laterad on the ventral surface of the olfactory nerve and

so pierces the glomerular zone in its extreme ventro-lateral angle. From this point it runs caudad and mesad toward the lamina terminalis on the extreme ventral surface of the hemisphere. In approaching the lamina terminalis the nerve separates into several bundles, a part of the one nearest the mid-line turning dorsad to break up in the region of the precommissural body in the rostral part of the lamina terminalis. Some of the fibers of this medial slip cross in the ventral part of the anterior commissure to the opposite side. Most of the nerve, however, which runs directly caudad on the ventral surface of the hemisphere to the level of the lamina terminalis, splits into several fascicles in the region of the anterior commissure. Here some of the fibers decussate, some break up in the preoptic nucleus, while others continue farther caudad—both direct fibers and those which have crossed in the anterior commissure. Some of the fascicles thus constituted retain their integrity until the level of the optic chiasma is passed, where running laterad and dorsad they break up in the hypothalamus. Other bundles, continuous with the nerve as it appears on the ventral surface of the hemisphere, run through the preoptic nucleus and passing dorsad and laterad at first through the hypothalmus turn sharply mesad to enter the extreme rostral and ventral part of the ansulate commissure in the interpeduncular region. Here the bundles break up or decussate in a region just ventral to the nucleus of the oculomotor nerve.

The following is a list of the preparations of the brain of Necturus which have been used in the study of the central relations of the n. terminalis:

Weigert method.................	1 horizontal	1 transverse	1 sagittal
Golgi method...................	40 horizontal		
Vom Rath method..............	2 horizontal	1 transverse	1 sagittal
Cajal method...................	3 horizontal		
Iron haematoxylin..............	2 horizontal		
Mallory's connective tissue stain.	2 horizontal	1 transverse	
Haematoxylin-fuchsin S.........	1 horizontal		
Carmine-Lyon's blue............		1 transvers	

The course of the n. terminalis near the ventral surface of the hemisphere is clearly apparent from figs. 1 and 2, which have

been made from photographs of horizontal sections of the brain of Necturus stained with iron haematoxylin. On the left side in fig. 1 the main bundle of the nerve can be followed continuously from the rostral part of the hemisphere past the lamina terminalis and into the preoptic nucleus. It will be noticed that the nerve lies quite near the ventral surface of the hemisphere. In large brains the nerve can be seen in the fresh condition, with the aid of a stereo-binocular microscope, most easily in the region of the lamina terminalis. In fig. 6 the nerve appears projected in red on a diagram of a median section of the brain of Necturus. Comparison of this figure and fig. 5 with figs. 7 to 18, transverse sections taken at the various levels marked on fig. 6, will show accurately the course of the nerve. Fig. 5 presents a drawing of a median section of the brain of Necturus which shows the form relations of the various parts of the thalamus and midbrain as they appear on the ventricular surface. The preparation from which the drawing was made was fixed in formaline-Zenker. Figs. 5 and 6 have been drawn to the same scale.

In passing from its ventro-medial position in the olfactory nerve to its situation in the ventro-lateral angle of the olfactory bulb, the n. terminalis, probably by reason of the glomerular growth in this region, is spread out so that it appears less compact in its transit of the glomerular zone than it does when the ventral surface of the hemisphere is reached. This fact makes it difficult, in brains stained with iron haematoxylin, Mallory's connective tissue stain or by Vom Rath's and the Weigert method, to observe whether or not the nerve really is continuous through the glomerular zone. By use of the Golgi method, however, where individual fibers may be followed, it is possible to trace actual fiber continuity of the n. terminalis through the glomerular zone. Figs. 20 to 25 show drawings of consecutive sections made from a brain treated by the Golgi method. From this preparation it is apparent that in the n. terminalis, as it occurs on the ventral surface of the hemisphere and farther caudad, we are dealing not with olfactory fibers rising in the olfactory bulb, but with fibers continuous from some point in the periphery

through the bulbar region. The possibility can not be excluded that some bulbar fibers join the nerve, but it is evident that such fibers are few.

In fig. 19 there appears a drawing made from a single horizontal section, 60 micra thick, prepared by the Golgi method. This section shows the way in which the n. terminalis, after having run thus far as a fairly compact fascicle, breaks up into smaller bundles in the region of the lamina terminalis and preoptic nucleus. Not only do the bundles break up into fibers which end among the dendrites of the cells of the precommissural body and preoptic nucleus which pervade this region, but there occurs also an interchange of fibers between bundles with subsequent reformation of fascicles which continue farther caudad. Fig. 3, from a photograph of a section of a brain prepared by Vom Rath's method and cut in a slightly different plane, shows the decussation of bundles of the n. terminalis in the anterior commissure. Some of the fibers of these bundles which have crossed end in the preoptic nucleus, but others join uncrossed fascicles which pass caudad to the hypothalamus and interpeduncular region.

In fig. 28 is shown a composite drawing made from consecutive sections, 50 micra thick, of a brain stained with haematoxylin and acid fuchsin. It illustrates the course of the bundles of the n. terminalis which reach the hypothalamus and interpeduncular region, bundles which are directly continuous with the n. terminalis farther cephalad and which include a part which has decussated in the anterior commissure. A bundle of the nerve has been seen to enter the postoptic commissure where it decussates. The subsequent course of this fascicle has not been determined.

Figs. 26 and 27 show two composite drawings made from a Golgi preparation in which actual fiber continuity is demonstrated in a fascicle which runs from the region of the anterior commissure to the interpeduncular region. The bundle breaks up in a region just ventral to the nucleus of the third nerve; and in the same section in which this occurs the fasciculus retroflexus of Meynert is seen to be ending. The fibers of these two fasciculi, accordingly, terminate in the same region. In this prepara-

tion the individual fibers of the fascicle which runs from the anterior commissure to the interpeduncular region could not be traced farther forward than the anterior commissure because the fascicle in question is not impregnated rostrad of this level. The portion, however, which is impregnated, maintains a position throughout the preoptic nucleus and hypothalamus exactly similar to that occupied by undoubted bundles of the n. terminalis as seen in other Golgi preparations and sections stained by iron haematoxylin or Mallory's connective tissue stain. In another series of sections prepared by the Golgi method there are impregnated several bundles of the n. terminalis which extend caudad of the post-optic commissure into the hypothalamus. One of these bundles, whose fibers pass continuously from the main part of the n. terminalis on the ventral surface of the hemisphere to the hypothalamus, seems identical in position, size and character of fiber with the fascicle noted above and shown in figs. 26 and 27. The impregnation, however, ends just cephalad to the rostral part of the ansulate commissure.

These facts indicate that there is actual continuity of fascicles of the n. terminalis from the periphery to the hypothalamus and interpeduncular region, and individual fibers are seen to pass from the periphery as far back as the preoptic nucleus and hypothalamus. The question as to continuity of individual fibers from the periphery to the interpeduncular region can not be answered definitely from the preparations now in hand, but such continuity seems quite probable. There is demonstrated, in this connection; fiber continuity in the bundle, described above, which can be traced from the anterior commissure to the interpeduncular region, a fascicle which very probably is continuous with the n. terminalis farther cephalad.

In fig. 4 appears a photograph of a horizontal section of the brain of Necturus stained with Mallory's connective tissue stain. The bundles, continuous with the n. terminalis farther cephalad, which reach the ansulate commissure in the interpeduncular region are seen in this section. There appear also in the ansulate commissure unmedullated bundles of the mammillo-peduncular fasciculi which must be distinguished from the fascicles of the n. terminalis in this region.

We see, then, that the n. terminalis in Necturus ends for the most part in the region of the preoptic nucleus, with a smaller amount of termination cephalad in the precommissural body and caudad in the hypothalamus and probably in the interpeduncular region. The main fascicles of the nerve split into smaller ones which divide again or separate into individual fibers. In preparations made by the Golgi method, where individual fibers may be studied, there can be noticed, often, fibers of the nerve which show a T-branching. Figs. 41, 42 and 43, drawings of Golgi preparations, show the way in which fibers of the n. terminalis often leave rather compact bundles and, turning toward the central grey of the preoptic nucleus, branch quite freely. In fig. 41 is shown the characteristic form of the cells of the preoptic nucleus among whose dendrites the fibers of the n. terminalis end in this region. It will be noticed that the character of the axones of these cells is different from that of the fibers which make up the n. terminalis.

AMBLYSTOMA TIGRINUM

In adult Amblystoma tigrinum, much as in Diemyctylus torosus, a part of the n. terminalis crosses the ventral surface of the hemisphere to the mid-line and the remainder runs quite directly caudad to the preoptic nucleus (fig. 29). The median part of the nerve breaks up into several fascicles and runs into the precommissural body. Not all of the bundles stop here, but some, passing caudad through the part of the anterior commissure just ventral to the rostral part of the third ventricle, break up about the cells of the preoptic nucleus in its rostral part, as shown in figs. 29 and 30. Some of these bundles decussate while piercing the anterior commissure. The lateral fascicle of the n. terminalis reaches the lateral part of the preoptic nucleus as shown in figs. 29 and 31. In Amblystoma the bundles of the nerve which reach the preoptic nucleus are much smaller than in Necturus. There can be seen, however, in sections of the brain of Amblystoma stained with Mallory's connective tissue stain, a small bundle (*a* in fig. 29) which continues caudad through the preoptic nucleus,

past the optic chiasma, and running dorsad, reaches the dorso-lateral part of the hypothalamus and the interpeduncular region. This fascicle is quite small and is followed with great difficulty, especially in the region of the optic tract and post-optic commissure, where the bulk of optic and commissural fibers is so great as compared with the condition of this region in Necturus. In adult Amblystoma the n. terminalis has been recognized in Golgi and Weigert preparations and in sections stained with Mallory's connective tissue stain.

In larval Amblystoma, as is seen in figs. 32 and 33, the nerve appears in essentially the same relations as in the adult. It can be recognized easily in specimens of 50 mm. but with no certainty in specimens of 30 mm. Fig. 32 illustrates the condition at the 44 mm. stage. It will be noted that here the bundles related to the precommissural body in the adult have not been observed. They are present at the 70 mm. stage as shown in fig. 33, but even in specimens of this length seem feebly developed.

DIEMYCTYLUS TOROSUS

In Diemyctylus torosus (figs. 35 and 36) the main part of the n. terminalis turns sharply toward the mid-line from its position in the postero-lateral angle of the olfactory bulb and running quite free on the ventral surface of the hemisphere, covered only by blood vessels, enters the substance of the hemisphere very close to its median surface. Here the nerve turns caudad and enters the rostral part of the precommissural body where the bundles spread out somewhat. A part of these bundles runs through the precommissural body and on reaching the anterior commissure a part decussates and the remainder, bending laterad, enters the region of the preoptic nucleus. These fascicles continue caudad through the preoptic nucleus to the dorso-lateral part of the hypothalamus and several can be followed still farther dorsad, into the interpeduncular region. These observations are based on two series of sections of the brain of Diemyctylus torosus stained with Mallory's connective tissue stain. Figs. 35 and 36 show composite drawings made from these two series.

It will be noted that in fig. 36, there occurs beside the median fascicles of the nerve, a lateral one which runs quite directly on the ventral surface of the hemisphere to the region of the preoptic nucleus. In this specimen this fascicle fuses with the median bundle in the region of the anterior commissure to form those fascicles which continue caudad to the hypothalamus and interpeduncular region.

AMPHIUMA MEANS

Fig. 34 shows a reconstruction made from horizontal sections of the brain of a specimen of Amphiuma, 42 cm. long. Here the n. terminalis appears among the fibers of the olfactory nerve at the extreme ventro-lateral angle of the olfactory bulb and from this point runs caudad in several fascicles to the region of the preoptic nucleus. Two of these bundles can be traced farther caudad to the hypothalamus and then dorsad to the interpeduncular region where they are lost in the ansulate commissure. These observations have been made on a single preparation of a brain fixed in formaldehyde and stained with iron haematoxylin and fuchsin S. In this specimen no fascicles were seen to enter either the anterior commissure or the post-optic commissure, the nerve maintaining an extreme lateral position throughout its course. In the region of the ansulate commissure, unmedullated fascicles appear, in addition to the bundles of the n. terminalis, which belong to the mammillo-peduncular fasciculi.

ACRIS GRYLLUS

The n. terminalis has been recognized in sections of the whole head of adult Acris gryllus (cricket frog) prepared by the Golgi and Cajal methods and in sections stained with toluidine blue and fuchsin S. Fig. 37 shows a reconstruction made from a series of Golgi sections. Here the nerve appears on the medial surface of the hemisphere, giving off several branches to the precommissural body and running finally to the region of the anterior commissure and preoptic nucleus. It can not be followed farther in the preparations at hand.

HYLA PICKERINGII (TADPOLE)

In these tree toad tadpoles the nerve has been noted in Golgi preparations and in sections stained with iron haematoxylin. In fig. 38 appears a reconstruction from a series of Golgi sections. Fibers of the nerve can be seen distributing to the precommissural body in the median portion of the hemisphere. The main bundle, however, runs caudad to the region of the anterior commissure where it breaks up in the preoptic nucleus.

RANA CATESBIANA (TADPOLE)

Fig. 39 shows a reconstruction of the n. terminalis in a tadpole of the bull-frog, 145 mm. long. The brain was prepared by the Weigert method. Here we see that the n. terminalis, crossing the glomerular zone in its ventro-lateral part, runs to the medial border of the hemisphere, as in Diemyctylus and Amblystoma. There is indication of the splitting off of several small bundles to the precommissural body, but the main part of the nerve runs caudad to the region of the anterior commissure, where it decussates and splits up in the preoptic nucleus.

BUFO LENTIGINOSUS AMERICANUS

Fig. 40 presents a reconstruction made from a series of sections of the brain of a toad stained with Mallory's connective tissue stain. The nerve appears rostrad among the olfactory fibers and glomeruli and turning a little toward the mid-line runs caudad to the region of the anterior commissure. Here the bundles break up, some of them decussating and others disappearing in the preoptic nucleus.

The nervus terminalis as described above for Necturus is considered to be homologous with the nerve in selachians, dipnoans, teleosts and in the frog. This homology follows on consideration of the central course and distribution of the fibers and because of the central independence of these fibers from olfactory fibers rising in the olfactory bulbs.

In Necturus, where there is little marked development of the optic and other special senses, it is probable that the nerve exists in primitive relations; that is, its course and distribution in the brain are not so much obscured by the other factors present as is the case in the frog and most of the fishes in which the n. terminalis has been described. The central connection with the preoptic nucleus in Necturus seems quite like that of selachians and dipnoans; but the fascicles which have been traced to the hypothalamus and interpeduncular region have not been encountered elsewhere. Further research will show, either that this condition is peculiar to Necturus, Diemyctylus, Amphiuma and probably to Amblystoma, or that it occurs likewise in other forms, more obscure perhaps, because of the greater development of other elements in these regions. It must be borne in mind that individual fibers of the n. terminalis have not been traced as such from the periphery to the interpeduncular region, but that fascicles continuous with the nerve cephalad reach this mesencephalic level.

A comparison of the findings presented here indicates that in three tailed amphibians, Necturus, Diemyctylus and Amphiuma and probably in a fourth, Amblystoma, there exists this mesencephalic connection of the n. terminalis. The principal central connection of the nerve, however, not only here in amphibia but also in fishes, seems to be with the preoptic nucleus, with a minor relation to the precommissural body which varies in amount in different forms. A consideration of the course and distribution of the fascicles of the n. terminalis in the brain of larval Amblystoma shows that the main bundles run directly from the olfactory nerve through the bulbar region to the preoptic nucleus. The absence of the fascicles which run to the precommissural body in young specimens indicates that these bundles in the adult arise later than the bundles to the preoptic nucleus. This fact, when considered in connection with the simple condition in Necturus, may lead us to believe that marked connection of the nerve with the precommissural body is not one of its primitive relations.

In view of the quite evident connection of the n. terminalis with the forebrain, Johnston ('06, '09) has expressed the belief

that we have here a telencephalic 'somatic sensory' nerve. The connection of this nerve in urodele amphibia with other segments of the brain in addition to the telencephalon must now be considered in its segmental valuation.

Edinger ('08, p. 215), Herrick ('10, p. 469) and Johnston ('11, p. 48) have suggested that in the epithalamus (habenulae) we have a correlation center for olfactory, optic and somaesthetic impulses connected with feeding reactions and the 'oral sense.' The fact that the fasciculus retroflexus of Meynert, the main discharge pathway from the habenulae, and a part of the n. terminalis, coming probably directly from the peripheral nasal region, end practically together in the interpeduncular region, seems of significance in this connection.

The course and distribution of the nerve as plotted for Rana catesbiana, Acris gryllus, Hyla pickeringii and Bufo lentiginosus americanus correspond quite closely to the condition as described by Herrick ('09) for the frog. His finding of 'terminal arborizations' of fibers of the nerve in the tissue adjacent to the lamina terminalis is here confirmed in Hyla pickeringii as is shown by fig. 38. In all the anura in which the nerve has been described most of the fibers seem to reach the preoptic nucleus with a few splitting off from the main part of the nerve farther cephalad to end in the precommissural body.

There has been noted in two specimens of Diemyctylus torosus, a variation in the exact course of the bundles of the n. terminalis. Such variations have likewise been encountered in Necturus, but have not been such as to alter the essential course and distribution of the bundles of the nerve. Differences frequently occur in the compactness and exact course of the bundles on the two sides of the same brain. A difference may frequently be noted and in the size of the brains of two individuals of the same length and in the relative size and shape of the various brain segments.

In adult Necturus and larval Amblystoma search has been made along the olfactory nerve and about the nasal capsule for the 'ganglion' of the n. terminalis. No cells have been found which can at present be regarded as actually related to this nerve. In larval Amblystoma of 40 to 60 mm. some scattered cells have

been observed in the olfactory nerve, about midway between the olfactory bulb and nasal capsule, which, by reason of their shape, size and chromidial content, appear much like ganglion cells. Their number, however, is small. Work on the peripheral relations of the n. terminalis in amphibia is in progress, the results of which will appear at a later date.

In an examination of the olfactory nerve of adult Necturus there have been found a few scattered cells whose contour and processes make them appear much like nerve cells. These cells have been observed not only in the olfactory nerve but also in the connective tissue surrounding the nasal sac and in the meninges of the brain in all its parts. On close examination the cytoplasm of these cells surrounding the nucleus and contained in the long branching processes, is seen to enclose sharp granules rather uniformly distributed which stain with the basic dyes (figs. 44, 45, 46). These granules stain metachromatically with toluidine blue and give no positive test for iron by McCallum's method. In Amblystoma larvae of thirty millimeters and over (fig. 46), the granules are relatively larger in proportion to the size of the cell and not so numerous as in adult Necturus. The granules of these cells in adult Necturus stain intra vitam with neutral red and methylene blue, with neutral gentian, toluidine blue and violet 5B after fixation in formaline-Zenker, and can be recognized in Weigert, iron haematoxylin, Vom Rath, Golgi and Cajal preparations. They are not nerve cells and correspond undoubtedly to the 'clasmatocytes' of Ranvier ('00), which are really mast cells, as Maximow ('02, '05) has definitely shown.

SUMMARY

1. The presence of the n. terminalis has been noted in the brains of Necturus maculatus, Diemyctylus torosus, Amphiuma means, Amblystoma tigrinum (larval and adult), Rana catesbiana (tadpole), Acris gryllus, Hyla pickeringii (tadpole) and Bufo lentiginosus americanus. A portion of the nerve in Necturus has been seen previously by C. L. Herrick ('93) and described and figured as an olfactory tract by Kingsbury ('95).

2. In all the forms above mentioned in which the central course of the nerve has been described the main connection of the nerve is with the preoptic nucleus. In Necturus maculatus, Diemyctylus torosus, Amphiuma means and probably in Amblystoma tigrinum, fascicles of the nerve have been traced to the hypothalamus and into the ansulate commissure in the interpeduncular region.

3. It has been shown that the n. terminalis in Necturus is composed of fibers which are continuous from some point in the peripheral nasal region, through the glomerular zone and bulbar formation, to the ventral surface of the hemisphere and farther caudad to the preoptic nucleus and hypothalamus. Fiber continuity has also been demonstrated in a fascicle which runs from the anterior commissure to the interpeduncular region, ending in the same section with the fasciculus retroflexus of Meynert from the epithalamus (habenulae). The fibers of this bundle, if not directly continuous with those of the n. terminalis, rise in a region in which fibers of the n. terminalis end. It follows that in the interpeduncular region we have ending together, the discharge pathway from the olfacto-somatic ('oral sense') correlation center in the epithalamus, and fibers intimately connected with or probably continuous with fibers of the n. terminalis which come from the peripheral nasal region.

4. End processes of fibers of the n. terminalis in the preoptic nucleus have been described; processes often quite freely branched.

5. Cells which occur in Necturus and larval Amblystoma, in the olfactory nerve, about the nasal capsule and in the meninges of the brain, which appear much like nerve cells, have been shown to be mast cells of connective tissue, the 'clasmatocytes' of Ranvier.

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ABBREVIATIONS

c. a., commissura anterior.
c. hip., commissura hippocampi.
com. ans., commissura ansulata.
com. po., commissura postoptica.
com. post., commissura posterior.
com. sup., commissura superior.
corp. precom., corpus precommissurale.
em. thal., eminentia thalami.
ep., epiphysis.
F., foramen interventriculare (Monroi).
foramen intervent., foramen interventriculare (Monroi).
f. b. t., basal forebrain tract.
fim., fimbria complex (see C. Judson Herrick '10, p. 427).
f. retrofl., fasciculus retroflexus of Meynert.
g. c., granule cells of the olfactory bulb.
gl., olfactory glomeruli.
hab., nucleus habenulae.
hyth., hypothalamus.
lat. f. b. t., lateral forebrain tract.
l. t., lamina terminalis.
m. c., mitral cells of the olfactory bulb.
med. f. b. t., medial forebrain tract.
n. med. s., nucleus medialis septi.
n. olf., nervus olfactorius.
n. olf. ant., nucleus olfactorius anterior.
n. po., nucleus preopticus.
nuc. magnoc., nucleus magnocellularis tecti.
n. term., nervus terminalis.
opt., optic tract.
pars dors. thal., pars dorsalis thalami.
pars. vent. thal., pars ventralis thalami.
prim. hip., primordium hippocampi.
r. po., recessus preopticus.
s. epen., septum ependymale.
s. m., sulcus diencephalicus medius.
s. shab., sulcus subhabenularis.
s. v., sulcus diencephalicus ventralis.
s. d., sulcus diencephalicus dorsalis.
taenia forn., taenia fornicis.
taenia thal., taenia thalami.
tectum mes., tectum mesencephali.
fasc. mam. ped., fascicle of the tractus mammillo-peduncularis.

EXPLANATION OF FIGURES

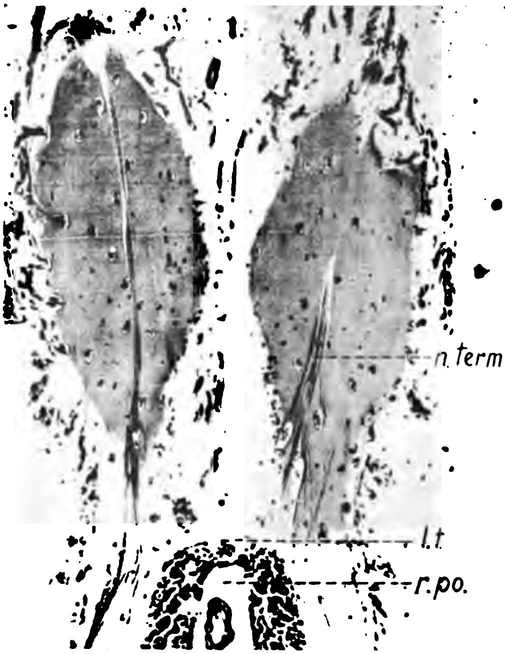
1 Photograph of horizontal section of the brain of Necturus, 15 micra thick, stained with iron haematoxylin and orange G after fixation in formaline-Zenker. The n. terminalis appears on both sides on the ventral surface of the hemisphere and caudad. × 30.

2 Photograph of a horizontal section taken from the same series and just ventral to that shown in fig. 1. × 30.

3 Photograph of a horizontal section of the brain of Necturus, 12 micra thick, stained by Vom Rath's method. Bundles of the n. terminalis appear in the anterior commissure. × 100.

4 Photograph of a horizontal section of the brain of Necturus, 15 micra thick, stained with Mallory's connective tissue stain after fixation in formaline-Zenker. The unmedullated bundles of the n. terminalis are seen in the region of the ansulate commissure. × 100.

The photographs shown in figs. 1 to 4 have been reproduced without retouching.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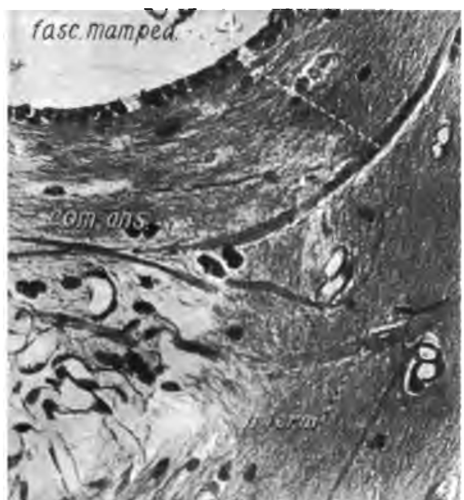
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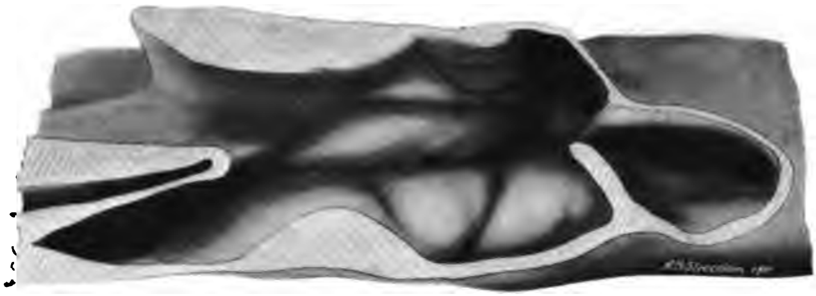
EXPLANATION OF FIGURES

5 Drawing of the brain of Necturus after median section showing the thalamus and midbrain as they appear on the ventricular surface. The brain from which this drawing has been made was fixed in formaline-Zenker and the drawing made with the aid of a stereo-binocular microscope. × 13.

6 Diagrammatic outline traced from drawing shown in fig. 5. The dotted lines represent the sulci and depressions on the ventricular surface. The course of the n. terminalis is indicated by the red line. The levels at which the transverse sections, shown in figs. 9 to 18, have been taken are indicated by the transverse lines. The numbers appearing therewith correspond to the numbers of the figures whose level is indicated. × 13.



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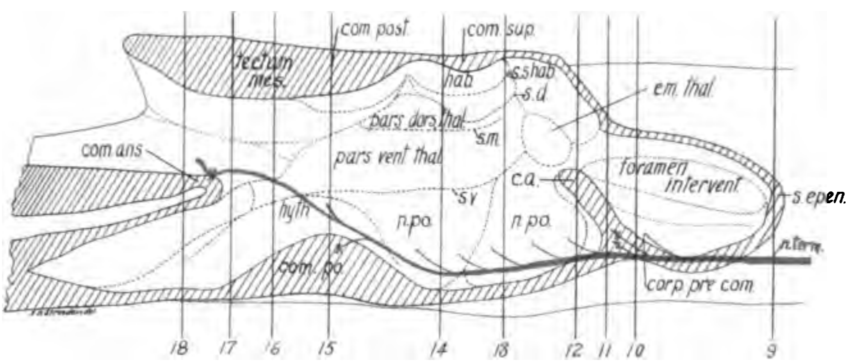
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EXPLANATION OF FIGURES

7–18 Drawings of transverse sections of the brain of Necturus, 15 micra thick, stained with Mallory's connective tissue stain after fixation in formaline-Zenker. All sections have been taken from the same series and the bundles of the n. terminalis are indicated in each. The relations of the medullated fibres in these drawings have been indicated after comparison with a series of sections prepared by the Weigert method. See fig. 6 for the levels at which sections 9 to 18 have been taken. All the drawings of transverse sections have been made to the same scale. × 17.

7 Section through the caudal end of the olfactory bulb.

8 Section through the rostral end of the primordium hippocampi.

9 Section just rostrad to the interventricular foramen, through the septum ependymale.

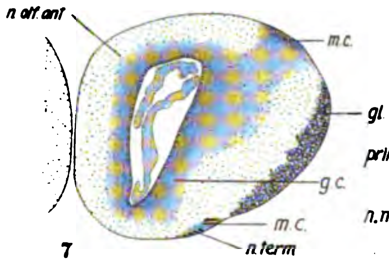
10 Section through the interventricular foramen and precommissural body.

11 Section through the rostral part of the anterior commissure.

12 Section through the caudal part of the anterior commissure.

13 Section through the extreme rostral end of the thalamus.

14 Section through the middle of the thalamus and optic nerve.



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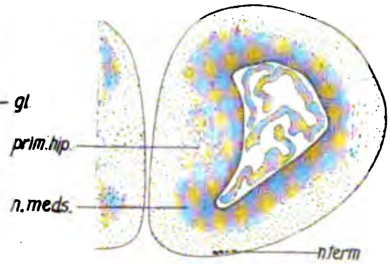

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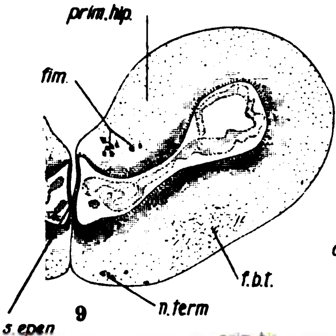

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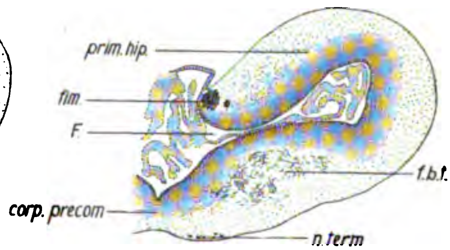

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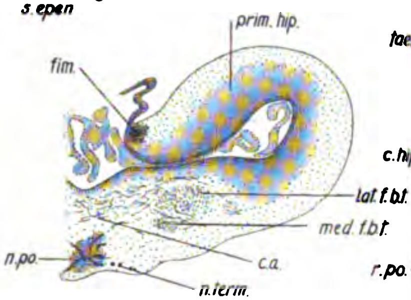

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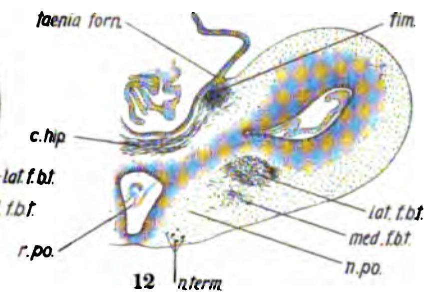

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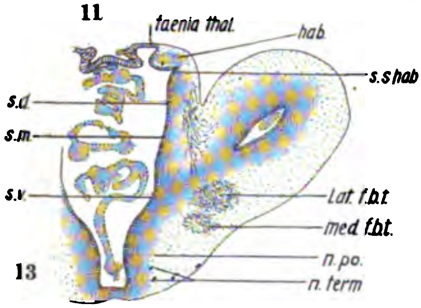

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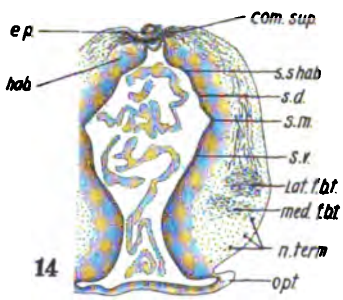

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EXPLANATION OF FIGURES

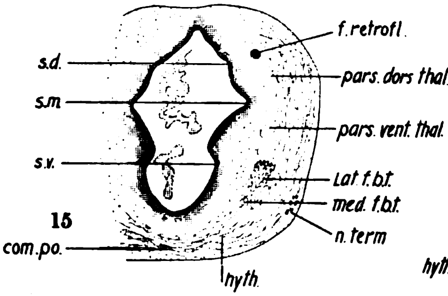
15 Section through the post-optic commissure.

16 Section through the rostral part of the mesencephalon.

17 Section through the middle of the mesencephalon.

18 Section through the tuberculum posterius and rostral part of the ansulate commissure.

19 Drawing of a single section of the brain of Necturus prepared by the Golgi method and cut 60 micra thick. The n. terminalis is impregnated. This figure shows the way in which bundles of the nerve break up in the precommissural body, anterior commissure and preoptic nucleus. The interchange of fibers between bundles is shown. The outer limits of the central grey are indicated by the dotted lines. Drawing made with the aid of the Edinger projecting apparatus. × 70.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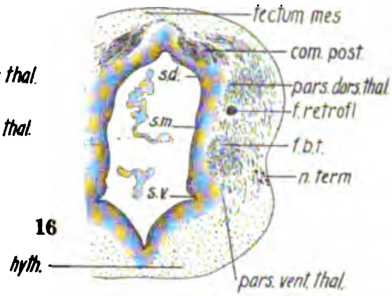
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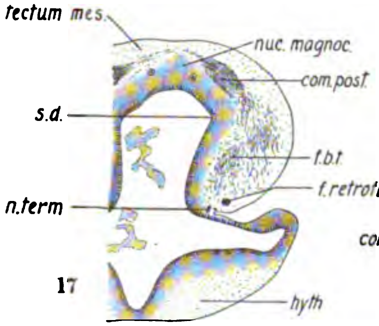
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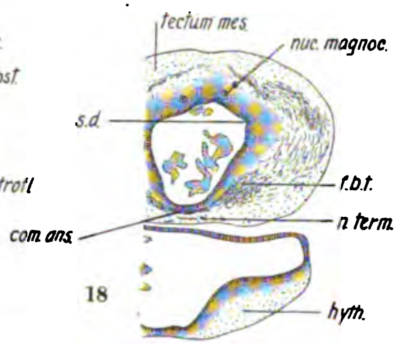
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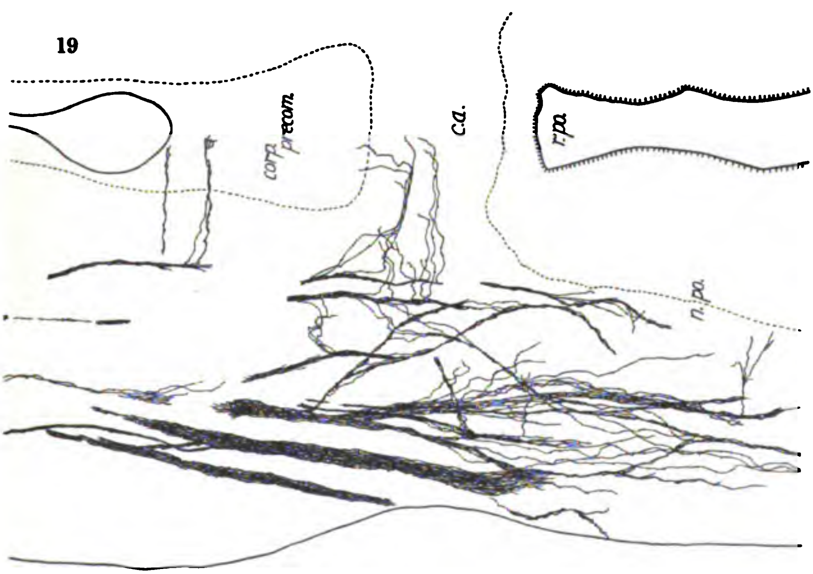
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EXPLANATION OF FIGURES

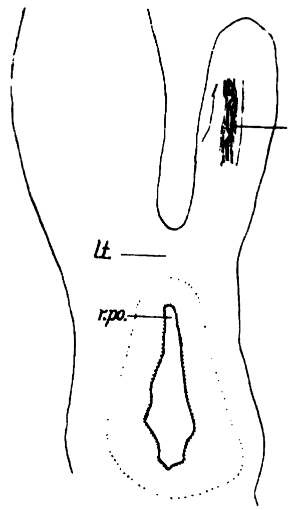
20–25 Consecutive horizontal sections of the brain of Necturus prepared by the Golgi method. Sections cut 60 micra thick. Drawings made with the aid of the Edinger projecting apparatus. × 15.

20 The n. terminalis appears on the extreme ventral surface of the hemisphere on the right side.

21 Branches of the nerve appear entering the precommissural body and anterior commissure and others, more lateral, running to the preoptic nucleus. The main bundle of the nerve is seen cephalad on the ventral surface of the hemisphere.

22 This figure shows the relation of the fascicles of the nerve in the region of the preoptic nucleus. See fig. 19.

23 In the region of the preoptic nucleus bundles appear which subsequently run caudad to the hypothalamus and interpeduncular region.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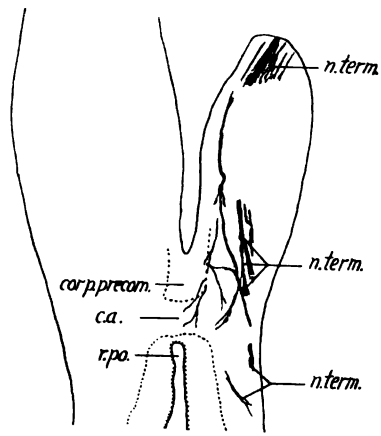
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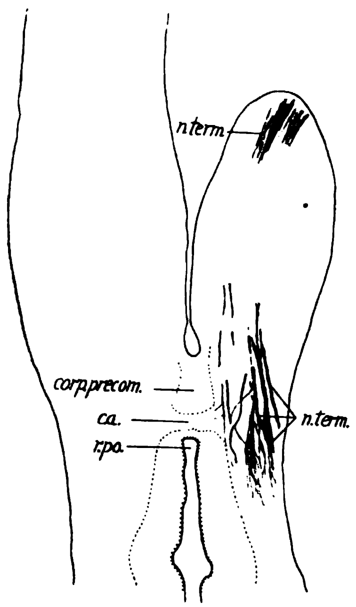
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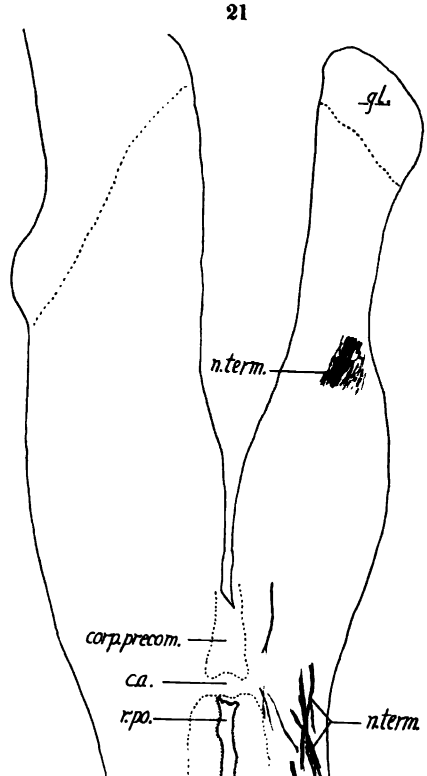
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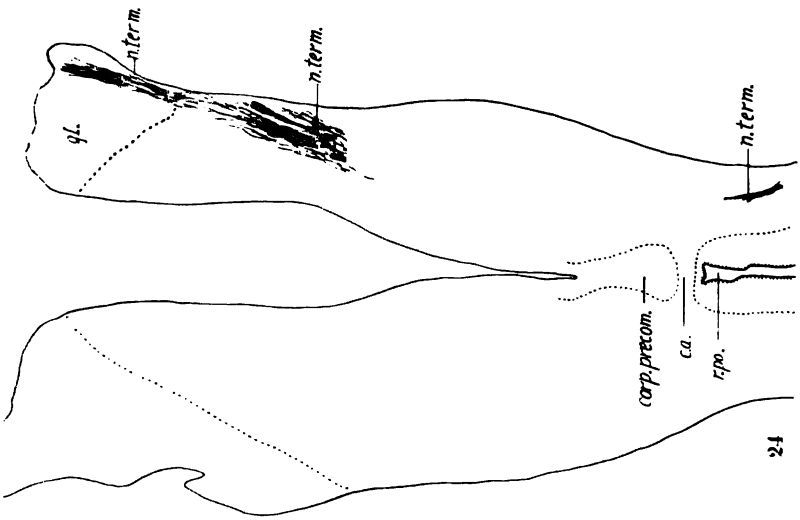
EXPLANATION OF FIGURES

24 This section shows the point at which the nerve pierces the glomerular zone. The caudal extent of the glomeruli is indicated by the dotted line.

25 Here the nerve appears in the olfactory nerve with some fibers still passing through the glomerular zone.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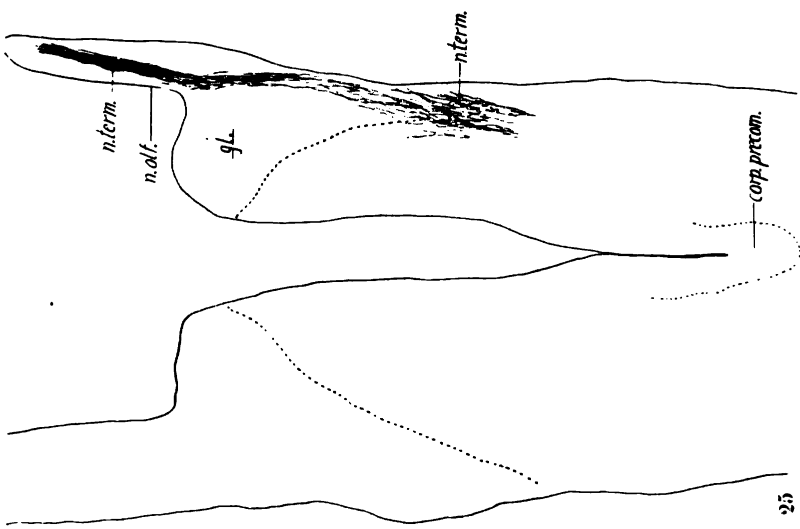
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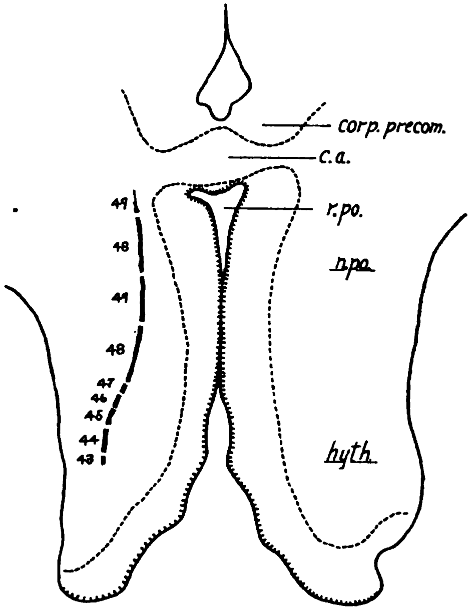
EXPLANATION OF FIGURES

In all the reconstructions which follow, except those made from Golgi preparations, lines are used as a convention in the representation of bundles of fibers and do not indicate individual fibers. All outlines were made with the aid of the camera lucida and where the outlines of two sections were used in the reconstruction their separation is marked by a dotted line. The number accompanying any segment of a bundle indicates the number of the section in which such segment was found.

26–27 Reconstructions made from consecutive horizontal sections of a brain of Necturus prepared by the Golgi method and cut 60 micra thick. These show the course and distribution of a fascicle, probably continuous with the n. terminalis cephalad, which is seen running from the anterior commissure to the interpeduncular region. Sections are numbered dorso-ventrad. The bundle contains about eight fibers. × 20.

26 Outline that of section 48.

27 Outline that of section 40. The fasciculus retroflexus of Meynert is shown ending together with terminals from the bundle shown in fig. 26.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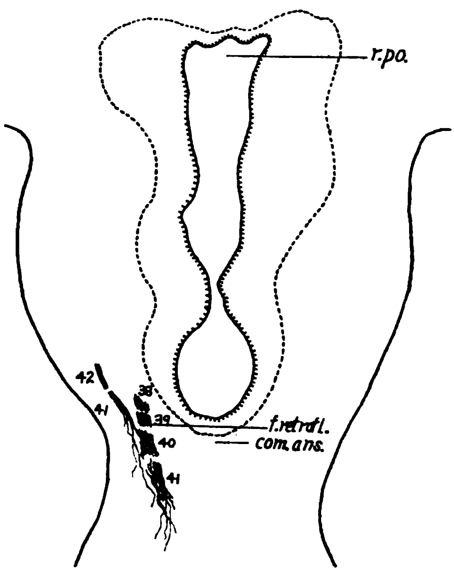
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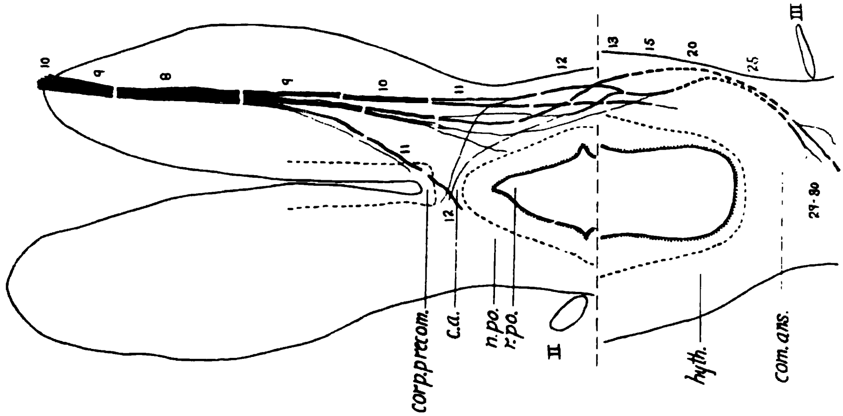
EXPLANATION OF FIGURES

28 Reconstruction of the n. terminalis in the brain of Necturus maculatus. Made from consecutive horizontal sections stained with haematoxylin and fuchsin S, cut 50 micra thick. Outline cephalad, section 11; caudad, section 30. Sections numbered ventro-dorsad. × 16.

29 Reconstruction of the n. terminalis in the brain of adult Amblystoma tigrinum. Horizontal sections cut 12 micra thick and stained with Mallory's connective tissue stain. Outline, cephalad, section 17; caudad, section 38. Sections numbered ventro-dorsad. × 50.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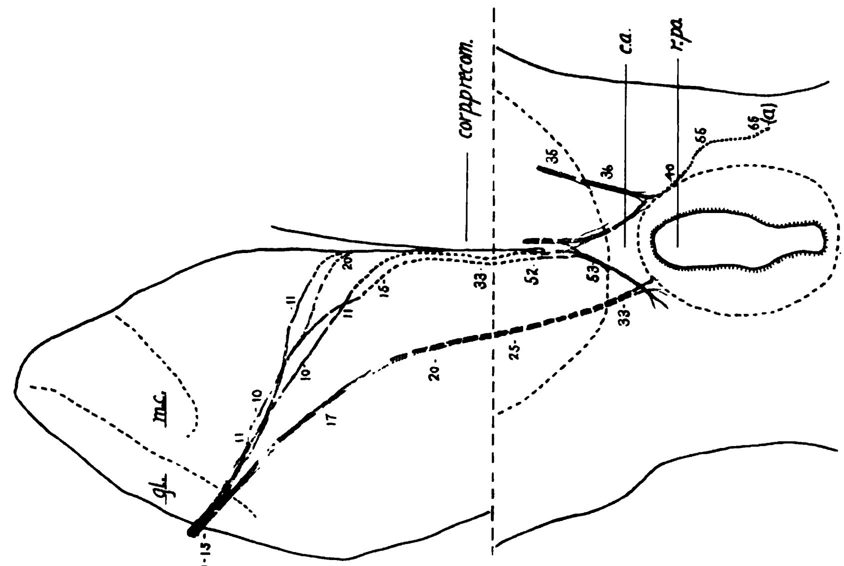
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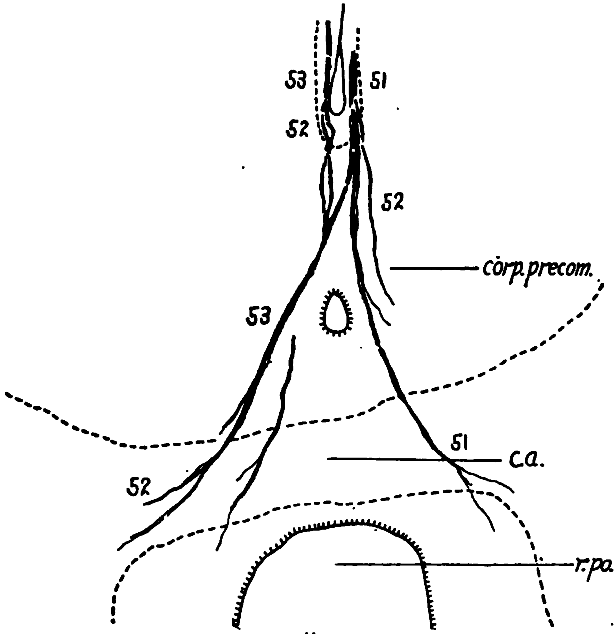
EXPLANATION OF FIGURES

30–31 Reconstructions made from the same series of horizontal sections of the brain of adult Amblystoma tigrinum stained with Mallory's connective stain and cut 12 micra thick. Sections numbered ventro-dorsad. × 105.

30 Reconstruction of bundles of the n. terminalis which run through the precommissural body to the anterior commissure and preoptic nucleus. Outline, section 53.

31 Reconstruction of bundles of n. terminalis which run directly on the ventral surface of the hemisphere to the preoptic nucleus. Outline, section 33.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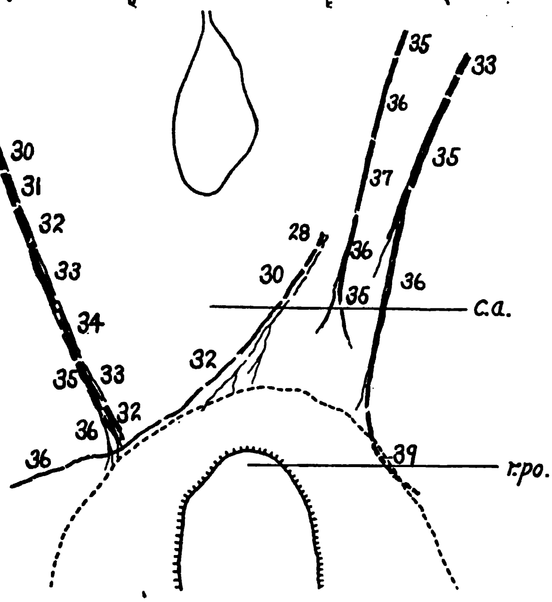
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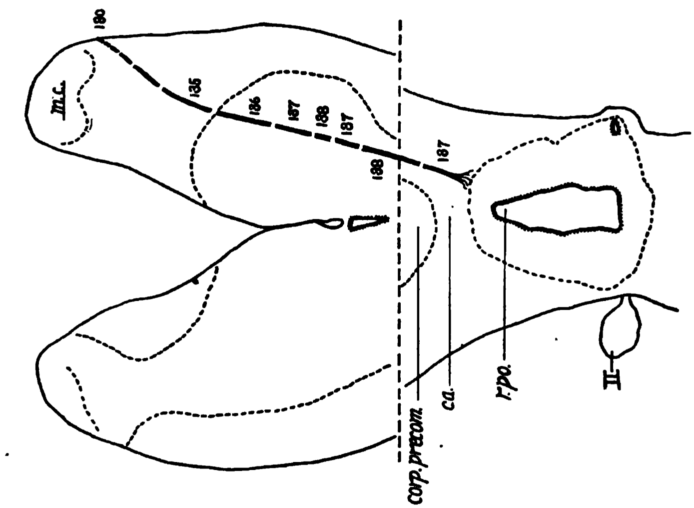
EXPLANATION OF FIGURES

32 Reconstruction of the n. terminalis in the brain of a specimen of larval Amblystoma tigrinum 44 mm. long. Horizontal sections 12 micra thick, stained with toluidine blue and fuchsin S. Outline cephalad, section 133; caudad, section 137. Sections numbered dorso-ventrad. × 50.

33 Reconstruction of the n. terminalis in larval Amblystoma tigrinum 70 mm. long. Horizontal sections 18 micra thick stained with Mallory's connective tissue stain. Outline cephalad, section 75; caudad, section 88. Sections numbered dorso-ventrad. × 34.



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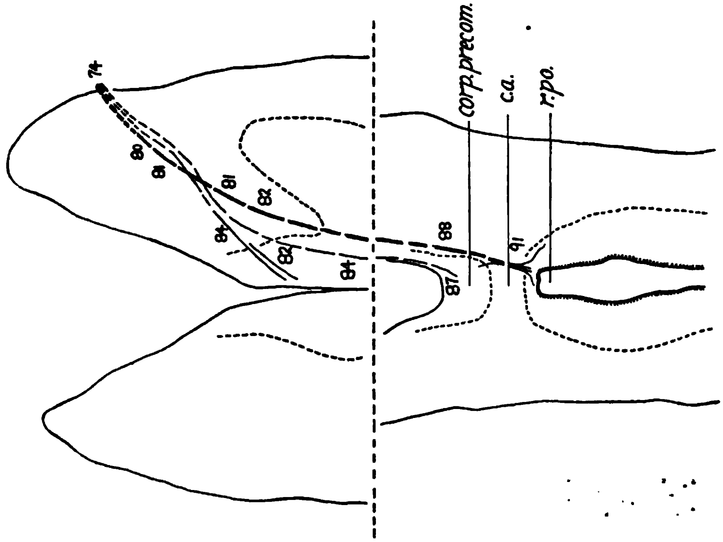

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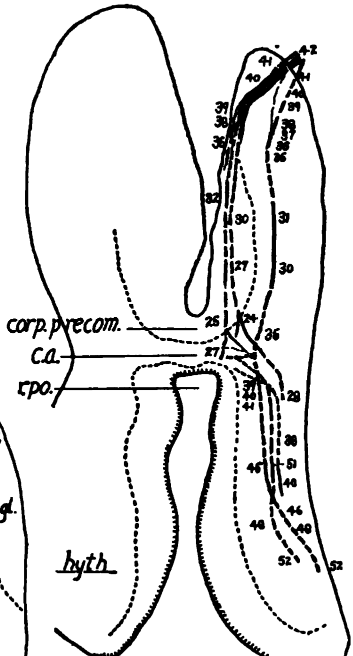
EXPLANATION OF FIGURES

34 Reconstruction of the n. terminalis in the brain of a specimen of Amphiuma means 42 cm. long. Made from horizontal sections, 15 micra thick, stained with iron haematoxylin and fuchsin S after fixation in formaldehyde. Outline cephalad, section 29; middle, section 49; caudad, section 91. Sections numbered ventro-dorsad. × 17.

35 Reconstruction of the n. terminalis in the brain of adult Diemyctylus torosus. Made from horizontal sections cut 12 micra thick and stained with Mallory's connective tissue stain. Outline cephalad, section 43; caudad, section 63. Sections numbered ventro-dorsad. × 34.

36 Reconstruction of a part of the n. terminalis in the brain of adult Diemyctylus torosus. Made from horizontal sections cut 12 micra thick and stained with Mallory's connective tissue stain. A defect in the series made impossible the plotting of the nerve farther caudad. Outline section 40. Sections numbered ventro-dorsad. × 32.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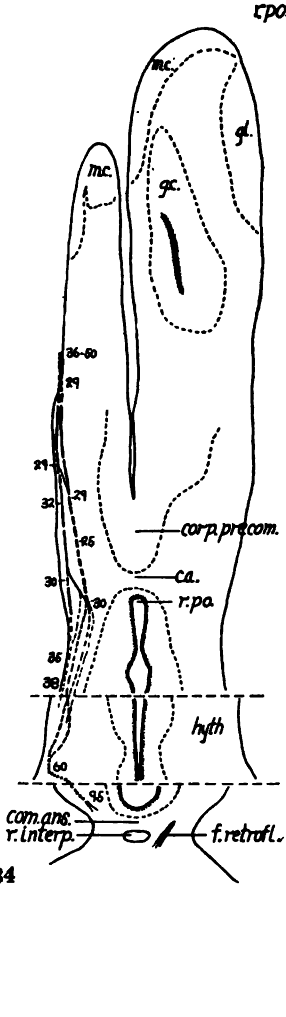
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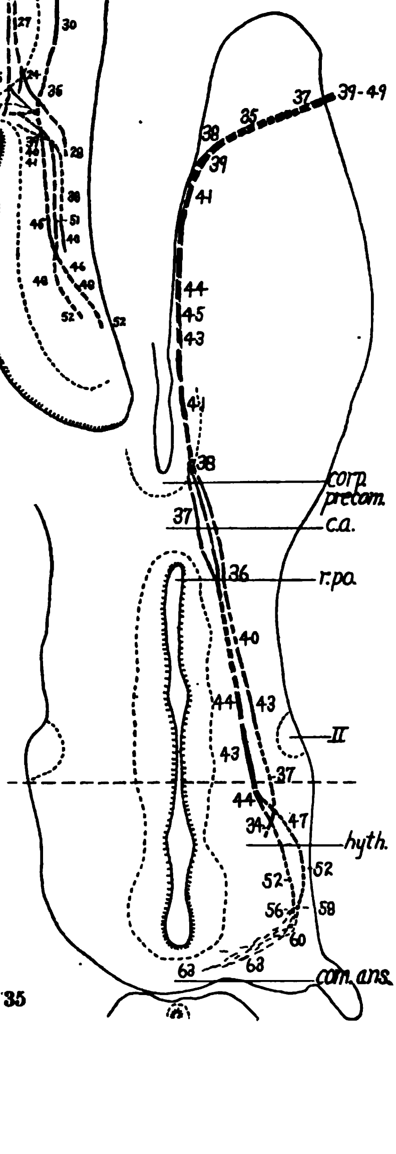
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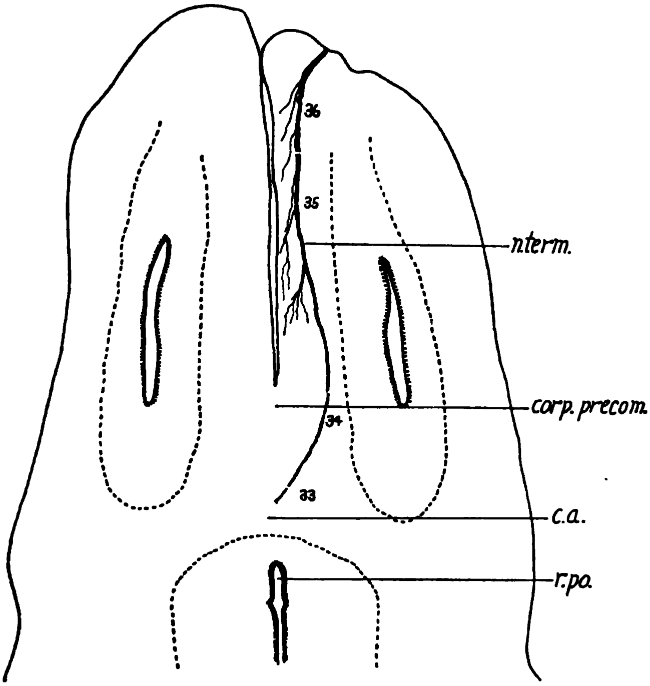
EXPLANATION OF FIGURES

37 Reconstruction of n. terminalis in the brain of Acris gryllus (cricket frog). Horizontal sections prepared by the Golgi method and cut 50 micra thick through the whole head of an adult specimen. Outline, section 35. Sections numbered dorso-ventrad. × 50.

38 Reconstruction of the n. terminalis in the brain of Hyla pickeringii (tadpole). Prepared by the Golgi method. Horizontal sections 60 micra thick, numbered dorso-ventrad. Outline, section 18. × 50.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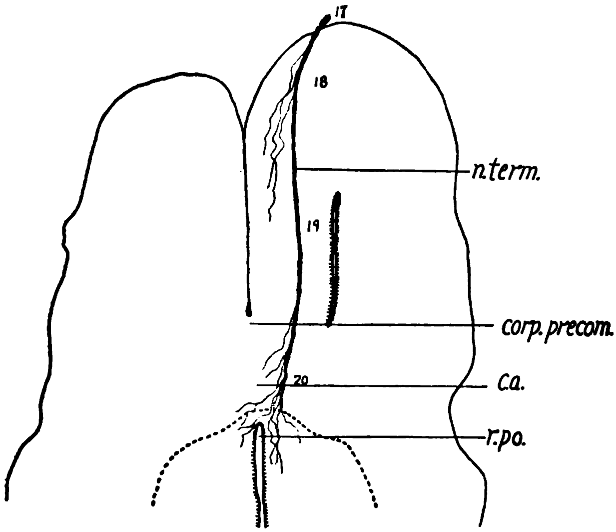
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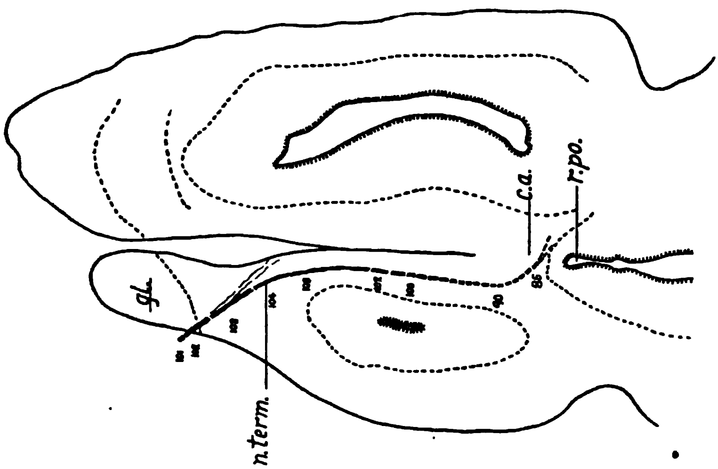
EXPLANATION OF FIGURES

39 Reconstruction of the n. terminalis in the brain of Rana catesbiana (tadpole, 145 mm.). Horizontal sections 10 micra thick stained by the Weigert method. Outline, section 102. Sections numbered dorso-ventrad. × 24.

40 Reconstruction of the n. terminalis in the brain of Bufo lentiginosus americanus. Horizontal sections stained with Mallory's connective tissue stain and cut 12 micra thick. Sections numbered ventro-dorsad. Outline, section 85. × 34.



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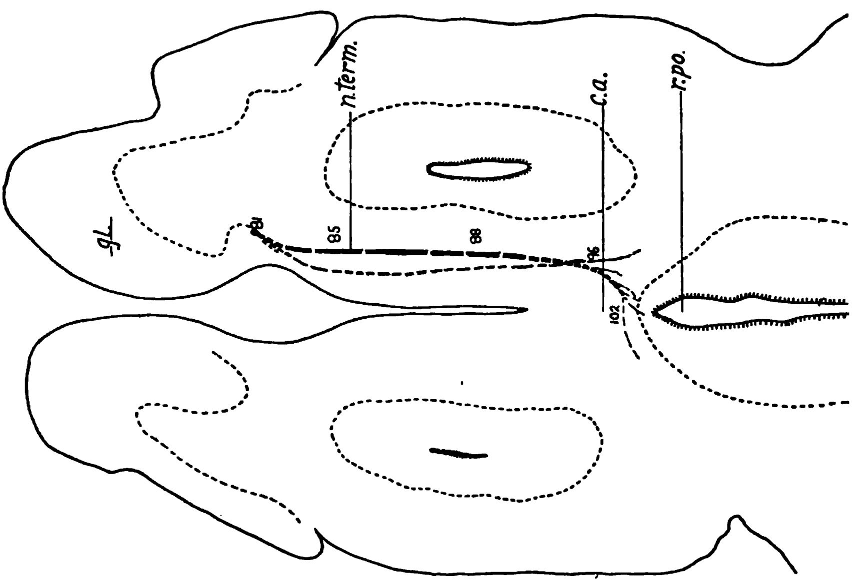

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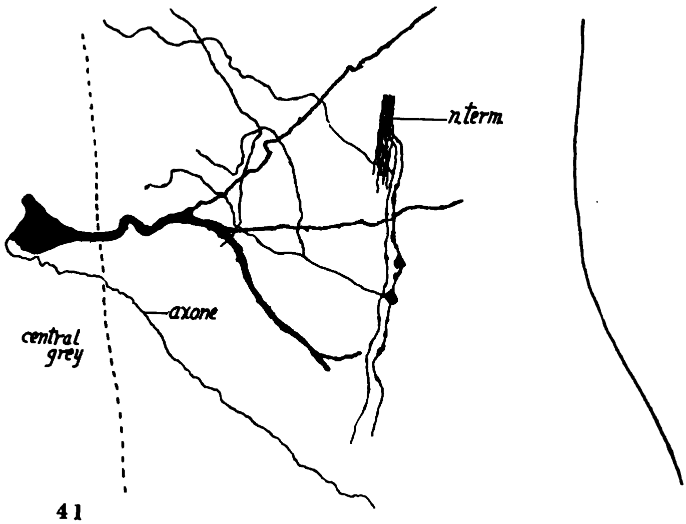
EXPLANATION OF FIGURES

41 Drawing of Golgi preparation of the brain of Necturus showing a bundle of the n. terminalis in the right preoptic nucleus. This section is horizontal; the lateral border of the central grey is indicated by the dotted line and the lateral surface of the preoptic nucleus shown by the unbroken line on the right. The method of branching of a fiber of a bundle of the n. terminalis is shown in its relation to the process of a cell of the preoptic nucleus. × 225.

42–43 Drawings of Golgi preparations of the brain of Necturus. Branches shown leaving bundles of the n. terminalis in the preoptic nucleus. × 225.



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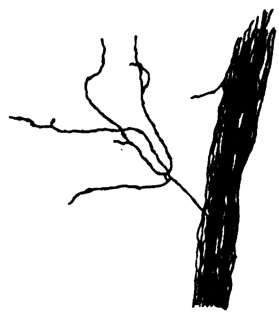

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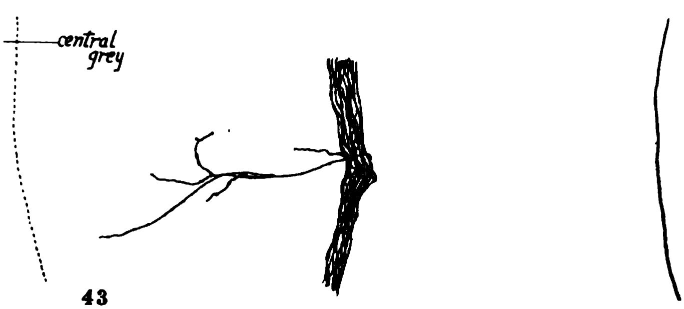

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EXPLANATION OF FIGURES

44–46 Mast cells in Necturus maculatus and Amblystoma tigrinum, the "clasmatocytes" of Ranvier.

44 Cell from meninges about the olfactory bulb of Necturus. Fixed in formaline-Zenker and stained with neutral gentian. × 425.

45 Cell from meninges on the ventral surface of the brain of Necturus. Fixed in Bensley's fluid and stained with toluidine blue. The cytoplasmic granules stain metachromatically. × 425.

46 Cell from the connective tissue medial to the nasal capsule of a larval Amblystoma tigrinum, 62 mm. long. Fixed in formaline-Zenker and stained with toluidine blue and fuchsin S. × 425.